University of Alberta

Bromus Inermis Leyss. Persistence and Invasion in Alberta Aspen Parkland

by

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ABSTRACT

Rough fescue prairie is currently threatened by invasion of *Bromus inermis* Leyss., an introduced cool season perennial forage species. The objectives of this study were to assess *Bromus inermis* persistence and invasion in response to specific environmental factors and to link those factors to potential mechanisms of invasion using two disturbances, at landscape, macro and meso scales. Within Alberta Aspen Parkland, *Bromus inermis* persistence and invasion at the landscape scale was assessed on two 25 year old pipeline rights-of-way (RoW) and invasion pattern and impact on the native plant community was assessed at a local site undergoing invasion. The results indicate that *Bromus inermis* persists and does invade where it is introduced, regardless of environmental variation. The impacts of invasion include reductions in native plant community diversity and loss of the dominant native species.

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I. INTRODUCTION

1. INVASION ECOLOGY

Richardson et al. (2000) define invasion as spread into areas away from sites of introduction. Biotic invasions occur when a nonindigenous species, dispersed beyond its native range, establishes in the new locale, reproduces and forms a persistent naturalized population, and finally invades surrounding communities (Lonsdale 1999, Mack et al. 2000). Invasion is an unlikely outcome of introduction, given the dispersal and recruitment limitation inherent in many ecological communities, as well as the effects of stochastity in environmental variation on survival of new populations (Lonsdale 1999). Plant invasions provide an opportunity to study the outcome of species introduction at many levels, which is important given the potential ecological and economic impacts of alien invasive species (Vitousek et al. 1997, Levine et al. 2003). Studies of plant invasions most often focus on the susceptibility of plant communities to invasion, the ability of individual species to invade, the ecological impacts of invaders, and the underlying mechanisms by which those impacts occur (Lodge 1993, Parker et al. 1999, Levine et al. 2003). The results of such studies vary widely and are often species specific, highlighting the need for investigation of individual cases and better understanding of the effects of invasion (Parker et al. 1999).

1.1 COMMUNITY INVASIBILITY

1.1.1 Effects of Species Richness and Diversity

Elton (1958) first proposed the hypothesis that communities with low species richness would be most susceptible to invasion. Based on the theory that species-poor islands are more susceptible to invasion, Elton's theory of biotic resistance (1958) is still the most prevalent hypothesis in the literature concerning community invasibility. On an island, geographical isolation results in fewer colonization opportunities and the plant community is thought to be unsaturated with many empty niches available for colonization. Based on Elton's theory of biotic resistance (1958) the relationship between diversity or species richness and invasibility should be negative. Supported by a negative relationship (Fox and Fox 1986, Tilman 1997, Hector et al. 2001) and refuted by studies showing a positive relationship (Robinson et al. 1995, Stohlgren et al. 2002,

Stohlgren et al. 2003), it is clear that the relationship between diversity and invasibility is not a simple one, if it exists at all (Fridley et al. 2004). Spatial scale is important to consider because the ability of a richer community to exploit more resources is based on interactions between individuals and is most likely to be observed at small scales (Ortega and Pearson 2005). At larger scales, environmental variation, rates of propagule supply and variation in resource availability have greater influence on invasion success (Levine and D'Antonio 1999, Ortega and Pearson 2005). Fridley et al. (2004) suggest that the observed relationships, positive at large scales and negative at small scales, are sampling and statistical artifacts and that appropriate null models should be used to evaluate deviations from these expected patterns. In a theoretical study Moore et al. (2001) found that the relationship between species richness and invasibility depends, not on richness itself, but on mechanisms that result in gradients of richness. The results from that study suggest that richness is not indicative of saturation, as is the case with grass dominance in fertile grasslands. Given the uncertainty regarding the relationship between invasibility and diversity, species richness alone is not the best indicator of plant community invasibility (Lavorel et al. 1999, Moore et al. 2001).

1.1.2 Effects of Disturbance

Disturbance is thought to be a main factor influencing community invasibility (Hobbs and Huenneke 1992). Davis et al. (2000) proposed a theory of fluctuating resource availability whereby plant communities become more susceptible to invasion whenever there is an increase in unused resources. Thus, any factors that increase resource availability will also increase a community's susceptibility to invasion. These factors would logically include natural disturbances such as fire, grazing and presence of burrowing mammals as well as anthropogenic disturbances such as cultivation (Hobbs and Huenneke 1992). In partial support of the theory of fluctuating resource availability, Gross et al. (2005) found that invasibility increased with removal of vegetation cover and with removal of vegetation cover combined with nutrient addition; but invasion did not increase with nutrient addition alone. Burke and Grime (1996), Thompson et al. (2001) and Smith and Knapp (1999) also found increases in grassland invasibility with disturbance, which partially supports the theory of Davis et al. (2000). Conversely, Walker et al. (2005) found no relationship between disturbance, nutrient addition and invasibility in short tussock New Zealand grassland. They cite the importance of plant-

community-specific characteristics in preventing invasion. In a study of historical invasion in California grassland, Corbin and D'Antonio (2004) showed that competitive characteristics specific to the native plant community were sufficient to repel invaders and that disturbance allowed invasion by Eurasian annual dicots.

1.1.3 Effects of Community Structure

Community structure is considered important in determining plant community invasibility (Fox 1987, Lavorel et al.1999). Fox (1987) stated that the lack of a particular functional group in a community would facilitate invasion by species of that particular functional group. The existence of functional groups in itself has proven difficult to demonstrate experimentally (Wilson and Roxburgh 1994, Wilson and Gitay 1995) and the definition of functional groups has been shown to be dependent on growing conditions and habitat type (Dyer et al. 2001). Nevertheless, functional group diversity as a measure of community structure has been tested. The underlying hypothesis is that species are likely to invade if they represent a functional group that is not present in the community at the time of invasion. Von Holle and Simberloff (2004) found that diversity of functional groups defined by morphology did not have an effect on community resistance to invasion. Symstad (2000) found only weak evidence that resident species, this time defined by physiological traits, repelled species in similar functional groups. Conversely, Zavaleta and Hulvey (2004) found that during invasion, entire functional groups were lost more quickly than expected by chance, and that invasibility increased with decreasing species richness. Although this study supports the existence of a relationship between functional groups and invasibility, it is a rare example in the literature.

1.1.4 Summary

The effects of species richness and diversity as well as functional group richness and diversity on community invasibility are variable, dependent on scale, functional group definition and environmental variability. Conversely, the relationship between increased community invasibility and increased disturbance is well demonstrated. It is impossible, however, to disregard the effects of individual species and competition on the success of a specific invader in a specific community (Lavorel et al.1999). The effects of scale and type of disturbance are also important to consider (Brown and Peet 2003). The variable results of studies focusing on the relationship between diversity and invasibility and the

more concrete results on the effects of disturbance show that studies integrating the effects of scale, environmental variability and disturbance on community structure and invasibility are necessary in the field of invasion ecology.

1.2 CHARACTERISTICS OF INVADERS

Like generalizations regarding diversity and invasibility, generalizations regarding the characteristics of invasive species have proven to be difficult to make (Smith and Knapp 2001). Some general characteristics of invaders include: No specialized environmental requirements for germination, rapid seedling growth, self-compatible but not obligatorily self-pollinated, high seed output, high tolerance to a wide range of environmental variation and disturbance regimes, adaptations for short and long range dispersal, and ability to reproduce vegetatively if perennial (Newsome and Noble 1986). This list is not exhaustive; successful invaders may posses one or none of the above attributes while an introduced plant that never invades may possess every one of them (Newsome and Noble 1986). Bazzaz (1986) adds the importance of niche breadth for invaders that rely on disturbance and the importance of competitive ability for others. Regardless of the long list of attributes, the invasive potential of a particular species remains difficult to predict.

Many studies have indicated that no single trait or group of traits is responsible for invasiveness (Rejmanek and Richardson 1996, Radford and Cousens 2000). Furthermore, differences are usually species-specific and dependent on plant-environment interactions (Thompson et al. 1995, Stohlgren et al. 1999). Often, characteristics of invaders are similar to those of their native counterparts indicating that ability to respond to disturbance or short-term fluctuations in resource availability may be the source of competitive advantage (Thompson et al. 1995, Smith and Knapp 2001). Invaders also differ in the extent to which they invade. Ortega and Pearson (2005) distinguish between "strong" and "weak" invaders where strong invaders are capable of dominating the invaded community while weak invaders coexist in the community. Likely, many factors are at play in determining whether an invader is strong or weak in a given community, including physical size and growth rate, response to and impact on competitors, resource availability, and presence of natural control agents, as well as the physical environment (Shea and Chesson 2002). The combination of these factors is

termed "niche opportunity" by Shea and Chesson (2002) and represents a modern definition of ecological niche. The concept of niche opportunity takes into account the community and environmental effects on the species and the effects of the species on the community and physical environment at any given point in time.

1.3 IMPACTS OF BIOLOGICAL INVASIONS

Though most work on the impacts of biological invasion has been done at community and ecosystem levels (Levine et al. 2003), these impacts can actually be classified into five different categories: Impacts on individuals, genetic impacts, population dynamics, community dynamics and impacts on ecosystem processes (Parker et al. 1999, Levine et al. 2003). Further, within plant communities individual impacts, population dynamics, community dynamics and ecosystem impacts are well researched, while genetic impacts have not been greatly studied (Parker et al. 1999). Within plant communities, several studies show decreases in diversity and species richness with invasion (Martin 1999, Mack et al. 2000, Hooper et al. 2005) although the mechanisms behind such decreases are seldom elucidated.

Competition for resources in the forms of light, water and nutrients is the most widely accepted explanation for the impacts of invasion on community structure (Shea and Chesson 2002, Levine et al. 2003). Martin (1999) and Wyckoff and Webb (1996) suggested the importance of light competition to the impacts of invasion in forest ecosystems. Melgoza et al. (1990) and D'Antonio and Mahall (1991) showed decreases in soil moisture because of invasion, suggesting the invaders are superior competitors for soil water. Blumenthal et al. (2005) demonstrated that restoration in tallgrass prairie decreased invasion through increased competition for light, and for micro sites needed for germination and establishment.

The effects of biological invaders at the ecosystem level are economically and ecologically significant (Vitousek et al. 1997). Impacts at this level can alter nutrient cycling, hydrologic cycling and disturbance regime, thus changing ecosystem structure and function (Levine et al. 2003). Vitousek and Walker (1989) showed an increase in nitrogen (N) availability in volcanic soils following invasion by nitrogen fixing woody species. Mack (2001) suggested that exotic grasses change nutrient availability through alteration of the disturbance regime and Evans et al. (2001) showed decreased N

mineralization rates as a result of decreased litter quality following invasion by *Bromus tectorum* L. While it is well demonstrated that nutrient cycling often changes because of invasion (Ehrenfeld 2003, Hook et al. 2004), the effects of those changes on community structure and the longevity of those effects are still unknown (Levine et al. 2003). Invading plants can also change local hydrology by changing the timing of maximum evapotranspiration (ET) due to physiology that differs from that of native species (Levine et al. 2003). Zavaleta (2000) showed increased ET following invasion; on the other hand, invasion by other species has decreased water use in the invaded community, contributing to increased leaching and runoff (Cline et al. 1977, Dyer and Rice 1999, Enloe et al. 2004). Invaders that alter disturbance regimes have potentially the largest and most irreversible impact (Vitousek 1990). Increased fire frequency and intensity (D'Antonio and Vitousek 1992, Brooks et al. 2004) due to increased litter production by invading species is one well documented outcome. While the impacts of invasive species can be relatively easily determined from experimental study, it is more difficult to determine the mechanisms behind them, as they are often species and community specific and operate at a temporal scale different from that of a study (Levine et al. 2003).

The information presented above shows that impacts of invasive species are responsible for changes in ecosystem processes and community structure. Given the demonstrated importance of disturbance in determining community invasibility (Section 1.1.2), it is possible to view invasive species as being better adapted to the new disturbance regime and thus better able to thrive in the disturbance affected community (MacDougall and Turkington 2005). MacDougall and Turkington (2005) found that dominant exotic grasses in the Garry Oak Savannah of British Columbia had limited susceptibility to fire suppression treatment, a noncompetitive process, whereas the subordinate native forbs and woody species responded most significantly to the treatments. In this study, the larger influence of environmental variation over that of competitive interaction supported the hypothesis that invaded communities are primarily structured by noncompetitive factors such as environmental variation and dispersal limitation that are less limiting for the invasive exotics studied.

1.4 CONCLUSIONS

The impact of introducing a particular nonnative species to a particular community is a function of the ecological characteristics of the community undergoing invasion and the invader. Different exotic species will invade different areas based on the niche opportunity in a given community and will have varying ecosystem level impacts, depending on the characteristics of the invading species. Lonsdale (1999) highlighted three aspects of invasion ecology that should be considered when studying the outcome of plant invasion: 1) Ecosystem properties, including disturbance regime and degree of disturbance, 2) dispersal rate of exotic species termed as propagule pressure, and 3) competitive characteristics of the native and exotic species. Robinson et al. (1995) stated that the background rate of species turnover, dispersal rate of the invading species and variation in the community resource base must be controlled to effectively formulate and test hypotheses regarding invasibility and invasion potential. Levine et al. (2003) state that it is as important to study the mechanisms behind invasion impacts as it is to study the impacts themselves. Before intense controlled experiments are undertaken, it is important to have the above information specific to the species of interest and the native plant community undergoing invasion so that appropriate questions are addressed. For that reason, background studies are a necessary step in the study of plant invasions.

2. *BROMUS INERMIS* LEYSS. INVASION IN ALBERTA ASPEN PARKLAND

In Alberta, less than 5% of *Festuca* (*Festuca campestris* Rybd. in the foothills and *Festuca hallii* (Vasey) Piper in the central parkland) dominated grassland of the Aspen Parkland and Fescue Grassland Ecoregions remains (Grilz and Romo 1995). Threats to remaining fragments of this ecosystem include cultivation, urbanization and exotic plant invasion. *Bromus inermis* Leyss. (smooth brome) is a commonly sown forage species in the parkland, fescue, and mixed grass prairie ecoregions. As an aggressive non-native, it has the potential to invade native ecosystems where it has been introduced (Nernberg and Dale 1997). Adverse effects of native plant community invasion by nonindigenous species are thought to include reduction in biodiversity (Hooper et al. 2005) and alteration of fundamental ecological properties including dominant species, nutrient cycling and plant productivity (Vitousek 1990, Parker et al. 1999). Much is understood

about *Bromus inermis* as a forage and hay crop, but further work is required to understand its pattern and mechanisms of invasion in rough fescue grassland if we are to reduce its invasive threat in the Aspen Parkland and fescue grassland ecoregions.

2.1 *FESTUCA CAMPESTRIS* AND *FESTUCA HALLII* GRASSLAND COMMUNITY

Festuca campestris and *Festuca hallii* (*Festuca* spp.) are the dominant C_3 grasses found in the black soil zone of Alberta (Moss and Campbell 1947). Both species are important winter forages for both cattle and wildlife because of high biomass production and because both species retain their nutritive value after they have cured (Willms et al. 1996). In this community, *Festuca* spp. almost completely excludes other species except under harsh conditions or in the presence of grazing or fire disturbance, due to the large dense tussocks that outcompete shorter species for light (Moss and Campbell 1947). Canopy interception is also thought to decrease soil moisture close to tussocks. These grasslands, with an average richness value of 25 species (Moss and Campbell 1947) can be considered a case where low species richness is a result of competitive dominance rather than the existence of empty niches as is often the case in relatively nutrient rich grassland (Mitchley 1996, Foster and Gross 1998, Moore et al. 2001). *Festuca* spp. reproduce primarily through tillering as seed production and long term viability of seed are low (Romo 1996). Anthropogenic disturbance is present throughout the Aspen Parkland ecoregion and the most common disturbances in *Festuca* spp. grasslands are grazing and mowing for hay (Moss and Campbell 1947). Mowing every two years reduces the competitive ability of *Festuca* spp. slightly as indicated by decreased tussock size and increased abundance of associated species, especially where moisture is limiting. Mowing more frequently and at decreased height produces a response similar to that expected under moderate to heavy grazing (Willms and Fraser 1992), which is a much more profound disturbance causing decreases in tussock size, density of distribution, and germinable seeds (Moss and Campbell 1947, Willms and Quinton 1995).

2.2 CHARACTERISTICS OF *BROMUS INERMIS*

A C_3, deep rooted, rhizomatous perennial, *Bromus inermis* is an important forage species in the Aspen Parkland Ecoregion of Alberta. First imported to Canada from

northern Germany in 1888, it was one drought survivor of the Great Depression and continues to be widely planted today due to its hardiness (Casler and Carlson 1995). In North America its range of distribution and use extends from Alaska to the Midwestern United States. It can survive extreme temperatures and periods of drought but grows best in deep, fertile, well drained silt to clay loam textured soils and is highly responsive to fertilization. *Bromus inermis* reproduces vegetatively and is a prolific seed producer (Brown 1997). Its seed can germinate over a wide range of soil temperature, moisture, and light conditions, which increases the probability of germination in varying environmental conditions as well as heterogeneous seedbed conditions (Grilz et al. 1994). *Bromus inermis* responds positively to defoliation, either from hay cutting or grazing, although regrowth is slow (Paulsen and Smith 1968). *Bromus inermis* and *Festuca campestris* and *Festuca hallii* are all cool season perennials capable of occupying the same range. Grazing disturbance negatively impacts *Festuca* spp., the dominant native species, and *Bromus inermis* is potentially able to take advantage of the new niche opportunity (Shea and Chesson 2002) and gain a foothold in the native plant community. The mechanisms by which *Bromus inermis* competes once present in the community are unknown.

3. SUMMARY

In Alberta and Saskatchewan Aspen Parkland, much research has been carried out on the eradication of *Bromus inermis* (Brown 1997), on factors relating to *Bromus inermis* as a forage crop (Donkor et al. 2002, Awada et al. 2003), on the general ecology of rough fescue grassland (Moss and Campbell 1947, Looman 1982), on the response of *Festuca* spp. to grazing (Willms and Fraser 1992, Willms and Quinton 1995), and on various physiological factors such as germination response to moisture and temperature (Romo 1996). These studies show that disturbance is likely an important factor during invasion by *Bromus inermis* as are the more general physiological requirements of brome. Further research needs to be done to demonstrate the invasibility of fescue grassland in order to determine the invasive potential and impacts of invasion by *Bromus inermis*.

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II . SMOOTH BROME PERSISTENCE AND INVASION IN THE ASPEN PARKLAND ECOREGION OF ALBERTA

1. INTRODUCTION

Grassland dominated by *Festuca hallii* and *Festuca campestris* within the Aspen Parkland once extended from central Saskatchewan to the western foothills of the Rocky Mountains in Alberta (Coupland 1961). Today, less than 5% of fescue grassland remains in isolated patches due to widespread cultivation for cereal and hay crops (Romo et al. 1990). Conservation values of rough fescue grassland include heritage, biodiversity, research, wildlife habitat, ecological reserves, aesthetics and recreation (Grilz et al. 1994). *Festuca hallii* and *Festuca campestris* are also important forage species for winter grazing by elk, deer and cattle (Willms et al. 1996). Conservation of rough fescue prairie is currently threatened by invasion of *Bromus inermis*, an introduced cool-season perennial forage species.

Commonly seeded as a forage species in the Aspen Parkland Ecoregion of Alberta and first introduced from Germany in the 1800s (Casler and Carlson 1995), *Bromus inermis* is a cool season perennial species capable of rapid spring growth and prolific rhizome, seed, litter and biomass production (Looman 1969). *Bromus inermis* is most commonly used as a forage species but is also planted in roadside ditches and is effective in erosion control (Casler and Carlson 1995). It was also commonly used as a reclamation species for oil and gas disturbances from the 1930s to the mid 1990s (Alberta Environment 2003). In response to moisture stress, *Bromus inermis* generally decreases shoot dry matter and increases defoliation intensity and frequency (Donkor et al. 2002) although it is considered drought and grazing tolerant (Brown 1997). Although germination of *Bromus inermis* seed is negatively affected by low soil moisture, it remains high compared to that of *F. hallii* and is largely unaffected by temperature (Grilz et al. 1994), allowing it to establish early in the season and maximize resource use before other species begin growing. In the Aspen Parkland and fescue grassland undergoing invasion, *Bromus inermis* is in competition primarily with *Festuca* spp. because they are the dominant native C_3 grasses.

Native to the grassland dominated portion of the Aspen Parkland, *Festuca hallii* and *Festuca campestris* are late seral, deeply rooted, densely tufted perennial grasses with

poor seed set, reproducing primarily through tiller production (Willms 1991, Stout et al. 1981). Yield of *Festuca* spp. is reduced by defoliation during the grazing season, although it is adapted to winter grazing (Johnston and MacDonald 1967, Willms et al.1996). Rough fescue is a dominant species, mainly excluding many other species (Moss and Campbell 1947). Germination of rough fescue seed is considerably lower than that of *Bromus inermis* across all ranges of soil moisture and temperature (Grilz et al. 1994) and grazing reduces seed production significantly (Willms and Quinton 1995). The response of rough fescue to other disturbances such as fire is highly variable, although fire is thought to be an important disturbance responsible for maintaining community diversity (Bogen 2003, Romo 2003). Growth begins early in the season and plants are dormant by early October (Brown 1997), which is comparable to the life cycle of brome, although *B. inermis* grows actively later in the season.

Many factors operating at a multiplicity of scales are likely responsible for invasion of rough fescue prairie by *Bromus inermis*. Understanding competition at small scales can help explain the mechanisms of brome invasion. Understanding the pattern of invasion at a landscape scale is important to prioritize eradication and conservation efforts. In addition, studying plant invasion at the landscape scale allows for understanding how the spatial distribution of resources and populations affect invasive spread (With 2002). Small scale experiments have led to contradictory results regarding the invasibility of plant communities (Fridley et al. 2004) and seldom have a broad range of applicability for land managers (Stohlgren et al. 2002). Nonetheless, small scale work is necessary to describe patterns and impacts of invasion to better formulate appropriate hypotheses regarding mechanisms of invasion induced change (Levine et al. 2003). Environmental factors possibly influencing plant invasion at a landscape scale include anthropogenic effects of disturbance, biotic factors such as dominant vegetation cover and abiotic factors such as soil characteristics (Stohlgren et al. 2002; With 2002). Conversely, at the scale of the individual plant, competition for available resources and resource allocation become more important in determining invasion success (Fridley et al. 2004). Studying invasion at both scales is necessary to understand the pattern and process of invasion.

2. RESEARCH OBJECTIVES

The objectives of this study were to assess *Bromus inermis* persistence and invasion in response to specific environmental factors and to link those factors to potential mechanisms of invasion using two disturbances, at landscape, macro and meso scales.

- At the landscape scale, specifically to evaluate canopy cover of *Bromus inermis* on and off two pipeline rights-of-way (RoW) in conjunction with slope, aspect, dominant vegetation cover and grazing impact (environmental factors).
- At the macroscale, specifically to characterize spatial distribution of *Bromus inermis* and native species in a rough fescue plant community undergoing *Bromus inermis* invasion from adjacent cultivated fields.
- At the mesoscale, specifically to quantify changes in canopy density, stem density, species composition and litter height at the invasion edge to better understand *Bromus inermis*'s competitive effects.

3. MATERIALS AND METHODS

3.1 STUDY SITES

3.1.1 General Study Area

All study sites were located in the Aspen Parkland Ecoregion, an intergrade between the boreal ecosystems to the north and grassland ecosystems to the south (Strong and Leggat 1992). Study sites represented the mosaic of soil types, topography and vegetation found within the ecoregion. The pipeline portion of the study is considered representative of the major vegetation cover types in the Aspen Parkland while the Ann and Sandy Cross Conservation Area (ASCCA) site is considered representative of the grassland portion of the Aspen Parkland (Figures 1 and 2).

The Aspen Parkland Ecoregion is one of the most productive agricultural zones in Alberta due to the combination of warmer temperatures and adequate moisture for biomass production (Strong and Leggat 1992). Consequently most of the arable land in the region is cultivated. Cattle often graze land unsuitable for agriculture. The hummocky moraine of the east-central portion of the region and the foothills to the west provide topographical constraints to cultivation and much of the remaining uncultivated parkland

exists because of these and similar limitations. The study sites were located on uncultivated land where topography prevented cultivation, although adjacent areas were often cultivated agricultural fields or improved pastures.

The soils of the ecoregion are typically dark brown to black chernozems in grassland areas and black and dark gray chernozems with gray luvisols in the aspen-dominated portion (Strong and Leggat 1992, Wyatt and Newton 1944, MacMillan 1987). On pipeline segments, soils were Orthic Black and Dark Brown Chernozems (Wyatt and Newton 1944) and the soils of the ASCCA were Orthic Black Chernozems (MacMillan 1987).

Annual precipitation ranges from 234 to 323 mm with July being the wettest month (Strong and Legatt 1992). Approximately 65% of annual precipitation is received during the growing season with the remaining 35% falling as snow during the winter. Average snow pack depth is highly variable due to the influence of topography, variation in vegetation cover and variable influence of chinook winds that induce mid winter ablation (MacMillan 1987). Colder temperatures combined with the lesser influence of chinooks and wind increase the duration of snow cover compared to that in the mixed grass ecoregion to the south. The chinook regime is slightly more important at the ASCCA site because of the sites proximity to the Rocky Mountains. Annual average temperatures in the Aspen Parkland range between 1.5 and 2.0 °C. Average daily temperature during the May to September growing season is 13.2 °C and from October to March is -2.5 °C. There are approximately 65 to 70 frost-free days each year.

The vegetation of the Aspen Parkland is a mix of forest, shrub and grassland communities. The forest communities occupy about 15% of the ecoregion and occur where there is enough moisture to allow tree growth (Strong and Leggat 1992). *Populus tremuloides* Michx. (trembling aspen) is the dominant species on north facing slopes, depressions and creek banks. Within the grassland component, shrub communities of *Symphoricarpos occidentalis* Hook. (snowberry), *Amelanchier alnifolia* Nutt. (saskatoon), *Rosa acicularis* Lindley (wild rose) and *Elaeagnus commutata* Bernh. *ex* Rydb. (wolf willow) have formed in gullies and draws where snow accumulates during the winter. Grassland communities are typically dominated by *Festuca halii* (Vasey) Piper (northern rough fescue), *Festuca campestris* Rydb. (foothills rough fescue), *Koeleria macrantha* (Ledeb.) J.A. Schultes (june grass), *Stipa* sp. (needle grasses) and various forbs, including *Galium boreale* L. (northern bedstraw) and *Geum triflorum* Pursh. (old man's

whiskers). On very dry sites, grassland communities are predominantly composed of *Stipa* sp., *Agropyron smithii* Rydb. (western wheatgrass) and *Agropyron dasystachyum (Hook.)* Scribn. (northern wheatgrass) (Tannas 2001). Important introduced species in the Aspen Parkland are *Bromus inermis* Leyss. (smooth brome) and *Poa pratensis* L. (kentucky bluegrass) (McClay 2004).

3.1.2 Pipeline Study Site

Two 25 year old pipeline RoWs (Figure 3) were used for the landscape scale portion of the study. The first RoW extends from 01-40-01 W4 north to 29-53-17 W4 (Study Pipeline 1). The second extends from 02-33-18 W4 north to 29-38-25 W4 (Study Pipeline 2). Evaluation occurred on 3,735 m on the first pipeline and 14,655 m on the second. Both pipelines were constructed between 1978 and 1981 for the transport of natural gas. Although construction details are not documented, topsoil salvage guidelines did not apply for pipeline construction and reclamation criteria were not in place at the time of construction. Standard practices of the day were likely followed so it can be assumed that soil was stripped in a single lift and replaced with little attention to resulting soil compaction and disturbance. Common revegetation practice involved seeding disturbed ground to commonly used forage species such as *Bromus inermis*. Note that although revegetation practices could not be verified, no other common forage species such as *Phleum pratense* L. were found on the RoW and native species were not seeded at that time.

In 1999 Alliance Pipelines initiated construction of a new pipeline to transport natural gas adjacent to Study Pipeline 1 and in 2000 BP Amoco commenced construction of a new line for the transportation of ethane adjacent to Study Pipeline 2. Soil handling and revegetation practices conformed to appropriate standards of the day and all native grassland and forest were seeded with a native seed mix. Guidelines and standards appropriate to this project include Guide for Pipelines: pursuant to the Environmental Protection and Enhancement Act and Regulations, (Alberta Environmental Protection 1994), Environmental Protection for Pipelines (Alberta Environment 1994), Revised Guidelines for Minimizing Disturbance in Native Prairie (Alberta Energy and Utilities Board 1996), and Manual on Soil Conservation and Pipeline Construction (Alberta Environmental Protection 1985). The final scenario was two 25 year old RoWs seeded to

Bromus inermis adjacent to two recently disturbed RoWs seeded to native species. Vegetation and soil types of pastures evaluated are given in Appendix A.

3.1.3 ASCCA Study Site

The ASCCA is located approximately 5 km SW of Calgary, Alberta and encompasses three sections (7E, 8W, 8NE, 8SE, 17, 18E twp 22 rg 02 W4) (Brown 1997). It was donated to the Fish and Wildlife Division of Alberta Forestry, Lands and Wildlife in 1987 and is managed by the Nature Conservancy of Canada. The ASCCA is topographically typical of the Rocky Mountain Foothill Ecodistrict of the Aspen Parkland Ecoregion with rolling topography underlain by sandstone (MacMillan 1987). Soils are typically Dark Gray and Gray Luvisols on plateaus and in valley bottoms where forest cover was once supported, and grade into Orthic Black Chernozems on south and west facing hillsides with predominantly grassland vegetation. Over time, much of the arable land at the ASCCA was cultivated for crop or hay production and native grasslands remain only on steeper south and west facing slopes (Brown 1997). There has been no grazing at the ASCCA since 1990. Prior to 1990 fields were either grazed or hayed in fall and mid-summer.

The study site is located on a south to southwest facing slope where *Bromus inermis* is invading from both a cultivated hilltop above and cultivated valley bottom below (Figures 4 and 5). *Bromus inermis* was initially seeded in 1944 with the last reseeding taking place in 1985 (Brown 1997). An initial reconnaissance assessment showed this site to be the only intact native grassland community at the ASCCA appropriate for a study of invasion. Other intact patches of native grassland were too small or on extreme slopes. The hillside plant community is characterized by *Festuca campestris*, *Poa pratensis* and *Danthonia parryii*. Soils are Orthic Black Chernozems (MacMillan 1987).

3.2 FIELD METHODS

3.2.1 Pipeline Field Methods

Environmental factors evaluated in this study were chosen so that the landscape scale niche of *Bromus inermis* could be better understood. Whether *Bromus inermis* preferentially invaded a certain type of landscape was of specific interest. Previous

research has shown *Bromus inermis* shoot dry mass and below ground dry mass decreased under heavy and frequent defoliation (Donkor et al. 2002). Grazing intensity was therefore chosen as a landscape level factor of interest. Shrub and tree cover is thought to decrease the cover of grasses (Li and Wilson 1998); thus vegetation cover type was designated another environmental factor of interest. Aspect has well known effects on soil temperature and moisture regimes as well as light intensity and duration (MacMillan 1987). Percent slope was chosen to better explain variation arising due to topographic position.

Sections of pipeline to be evaluated were restricted to uncultivated Aspen Parkland. Sites were selected through interpretation of air photos at a scale of 1:30 000 as well as examination of the pipeline alignment sheets for pipelines 1 and 2 provided by BP Amoco and Alliance (Alliance Pipelines Ltd. 1999, BP Amoco 2000). Air photos were used to exclude improved pastures and to show road access to the site. The vegetation description in the alignment sheets confirmed the presence of native vegetation typical of the Aspen Parkland Ecoregion. All pastures confirmed to be in uncultivated Aspen Parkland and accessible were evaluated regardless of length. Because all surveys were carried out on foot, access within reasonable walking distance was required. Some native pastures, specifically within CFB Wainwright, had to be excluded because of limited road access.

Pastures were defined by fencelines and were separated by cultivated fields, improved pastures or roads. Sections of pipelines in native pastures varied in length from 100 m to 1.5 km. 27 pastures totalling 18.3 km in length were assessed. Variation in length arose due to the pipeline route through portions of sections within townships. For example, the pipeline may have run through only the corner of one section and completely transected another section. Within each pasture all variables were evaluated at a 10 m scale, meaning that variation within that minimum length was not considered. This was done to minimize variation in the dataset caused by processes that operate at a small scale. All variables were recorded each time a change was observed in any variable over a greater than 10 m distance. The result was a number of variable length segments within each pasture for which all variables of interest were recorded (Figure 6). Factors were evaluated only on the side of the RoW undisturbed by new pipeline construction in 1999

and 2000 to avoid capturing variation due to recent construction. Sampling was carried out in July 2003.

Bromus inermis cover class (Daubenmire 1959) (Table 1) on the RoW and three meters away from the RoW on the undisturbed side of the pipeline was recorded at a 10 m scale as described above. The RoW was determined by the presence of a roach or raised ground over the buried pipeline. Dominant plant cover type was also recorded. Vegetation cover was classified into 14 dominant cover types that recurred over the landscape and were determined during a reconnaissance field trip (Table 2). Classification was determined by splitting the major cover types, grassland, shrubland and forest into more descriptive categories encountered in three different pastures. Grassland was separated into categories that described the dominant grass species most often encountered. Shrubland was categorized on the basis of the dominant grasses in the understorey and forest was classified on the basis of topography. Dominant vegetation cover was assessed in this way to minimize noise generated by capturing local scale variation in plant community composition.

Slope and aspect were measured with a clinometer and compass, respectively. Measurements were made each time variation occurred over a distance greater than 10 m.

Grazing impact occurred at the largest scale on the landscape of all environmental factors assessed. To maintain consistency and objectivity, grazing impact was assessed concurrently with all other variables. Grazing impact was determined visually, based on 1) presence of seed heads indicating the current grazing regime, 2) percent cover of litter indicating the grazing regime over the past three years and 3) species composition indicating grazing regime over the previous decade. Litter is defined as senesced vegetation from previous years above the soil surface. Species composition is defined as the presence of increasers versus the presence of decreasers. Increasers are defined as plant species that increase in the presence of grazing and decreasers are defined as species that decline under moderate to heavy grazing (Tannas 2001). A grazing impact matrix (Table 3) was used to assess grazing impact.

3.2.2 ASCCA Field Methods

To determine the competitive characteristics of *Bromus inermis* and its effects on rough fescue plant communities, six 225 m north-south transects were assessed on the south-facing hillside at the ASCCA. Transect length was determined by length of the slope and were placed systematically about 15 m apart. Rises and draws were present due to erosion on the hillside. Three transects were located in draws and three were located on rises to capture all topographical variation on the hillside. Species area curves were constructed in the field to ensure an appropriate amount of data was being collected. To construct the species area curve a 0.1 m^2 quadrat was placed in randomly selected locations in the study area. The species found were plotted on the y axis against the number of quadrats on the x axis. When new species were no longer being recorded the number of quadrats was deemed appropriate to capture most species in the community. For this study the optimum number of quadrats required in native prairie was 26 and each transect had about 46 quadrats.

Data were gathered at two levels of detail on all transects; an overall characterization of the invasion pattern on the hillside (macroscale), and a detailed characterization of invasion edges (mesoscale). At the macroscale, one 0.1 m^2 quadrat was placed every 5 m and percent ground cover, canopy cover by species, and litter cover were visually assessed only by the main researcher to prevent evaluator variability. Consistency was maintained by reference to diagrammatic representation of 5%, 10% and 20% cover in a 0.1 m^2 quadrat drawn on the back of the clipboard. Shannon-Weiner diversity, species richness (number of species) and evenness were calculated from species composition data.

At the mesoscale, a line transect was placed at three randomly selected edges of invasion on each hillside transect (Figure 7). Each line transect was placed perpendicular to the invasion edge and extended 50 cm into the *Bromus inermis* stand and 50 cm into the rough fescue stand with a transition area of varying length between because native plants and *Bromus inermis* intermingled over variable area in the transition zone. In some transects the invasion edge was very sharp and in others it was more diffuse. On average, mesoscale transects were 130 cm long. The number of stems per plant species in each 10 cm interval along the line transect was recorded. To evaluate canopy composition, height and vertical density, a metre stick was placed

vertically at 10 cm intervals along the line transect. Species in contact with the metre stick were identified and their corresponding height was recorded. Species identification followed Moss (1982), Tannas (2001) and Johnson et al. (1995).

3.3 STATISTICAL ANALYSES

3.3.1 Pipeline Statistical Analyses

Due to dependence between sample units, multi-colinearity among independent variables, and the variation inherent in landscape level effects, the entire data set could not be analysed. Multi-colinearity was inferred after running a 3 x 3 x 4 contingency table analysis on the explanatory variables alone and finding no independence among the variables. Lack of spatial independence is assumed because sample units are directly adjacent to each other (Hurlbert 1984). The independence assumption is inherent in all statistical methods, univariate (Zar 1999) and multivariate (McCune and Grace 2002). Lack of independence among sample units arose from spatial autocorrelation, which can be defined as random variables taking values at pairs of sampling locations that are more similar or less similar than would be expected if variables were randomly associated (Legendre 1993). Violation increases the chance of type I error in the case of positive autocorrelation and increases the chance of type II error in the case of negative autocorrelation. The data from the pipeline study is positively autocorrelated due to sample units within pastures being directly adjacent to each other. Multicolinearity between independent variables also decreases the validity of inference and is an important reason for not using the ANOVA procedure that assumes a linear model (Zar 1999). Nonparametric techniques were considered but the independence assumption is also inherent in these methods (McCune and Grace 2002). Log-linear analysis of 3 x 3 x 2 contingency tables was tried but the dependence within the data set invalidated the model.

In light of the correlative nature of the data set, the data were analyzed to answer a simpler question than initially posed in the objectives. *Bromus inermis* cover class on the pipeline and presence or absence of *Bromus inermis* off the pipeline were compared for two treatments: disturbed (pipeline RoW) and undisturbed (off the RoW). Given that *Bromus inermis* persists 25 years after introduction on the pipeline as evidenced by its presence irrespective of grazing regime, aspect, slope or vegetation cover type, the data

were analyzed to determine if *Bromus inermis* moves off the pipeline following introduction. The data were evaluated in a 6 x 2 contingency table to determine if the observed frequency of *Bromus inermis* presence and absence off the pipeline was independent of *Bromus inermis* cover class (Table 1). Only cover classes 1 to 6 were evaluated as there were only two cases where cover class was greater than 6. The p-value for the test was determined using the chi-square test statistic; α was equal to 0.05.

3.3.2 ASCCA Statistical Analyses

To characterize the *Bromus inermis* invasion pattern, quadrats were grouped using hierarchical agglomerative cluster analysis in PC Ord. The distance measure used was relative Euclidian and the linkage method was Ward's method (McCune and Grace 2002). The resulting dendrogram was scaled using indicator species analysis (ISA) following the method of Dufrêne and Legendre (1997). Significant indicator species for each group and the corresponding indicator value (IV) and p-value were reported (Table 4). Following pruning with ISA, approximately 60% of information remained according to Wishart's objective function.

Hierarchical cluster analysis is a process by which an n x n distance matrix is calculated by determining the distance between each pair of entities in the analysis, (McCune and Grace 2002) where n is the number of entities. In the case of the ASCCA data set, entities were quadrats. Groups are fused repeatedly using a criterion of minimum distance, in this case Ward's method, until all groups are fused. The resulting dendrogram showing each level of fusion is scaled by Wishart's objective function which measures the information lost in each level of clustering. The appropriate level of clustering must then be determined to obtain biologically meaningful groups. This is termed pruning the dendrogram.

Indicator species analysis (ISA) (Dufrêne and Legendre 1997) is a useful method for objectively pruning the dendrogram (McCune and Grace 2002). Using a priori groups of sample units, ISA calculates the proportional abundance of a specific species in a particular group relative to its abundance in all groups and is termed relative abundance (RA). Next, the proportion of sample units in each group that contain the species is calculated. This calculation is carried out for all species to obtain a sample unit by species matrix that is subsequently transformed to a matrix of presence-absence. The

relative frequency (RF) of the specific species is then calculated. Multiplying RA x RF as percentages results in an indicator value (IV) between 1 and 100. Species with IVs close to 1 are considered poor indicators while species with IVs approaching 100 are considered the best. Statistical significance is evaluated using a Monte Carlo method that randomly assigns sample units to a priori groups 1000 times, performing the above calculations each time. The probability of the IV being obtained by chance is the proportion of times the IV calculated from the randomized data set equals the IV from the actual data set.

ISA is used to prune the dendrogram by subjectively selecting a maximum acceptable number of groups (i) and running the analysis on each set of groups (i groups to 2 groups). For this data set, a maximum number of 10 groups out of a possible 277 were selected and thus the analysis was run on sample units grouped by hierarchical agglomerative cluster analysis into 10 groups, 9 groups, 8 groups and so on. Dufrêne and Legendre (1997) found that if sample units were too finely divided by cluster analysis, indicator values would be low and associated p-values would be high. An identical trend arose when clusters were too large due to within-group heterogeneity. At an optimal level of clustering, IVs peak, and the position of this peak varies according to species. The optimal level is determined by the number of clusters that result in the lowest average p-value or the largest number of significant indicators (McCune and Grace 2002). For this analysis, the lowest average p-value occurred where ISA was carried out on 4 clusters and the most significant indicators occurred when 3 clusters were used for the ISA. Examination of the data set showed that the 4^{th} cluster was a very small (11 sample units) subset of native vegetation with little biological significance at the scale of interest. Therefore, only three clusters were used.

Differences in measured variables between groups were characterized using the Kruskal-Wallis ANOVA by ranks. The same procedure was used for the invasion edge data. Data were assessed for normality using normal probability plots as well as the G1 and G2 statistic for skewness and kurtosis. Homogeneity of variance was assessed using Levene's test. The normality assumption, homogeneity of variance assumption or both assumptions were violated in almost every case and log, square root and arcsine transformations did little to remedy the violation. Zar (1999) states that the ANOVA procedure is robust to violation of the assumptions concerning homogeneity of within-group variance and normality, but becomes less robust to the homogeneity of variance

violation if n is unequal. Because sample sizes were unequal and one or both important assumptions of ANOVA were violated, nonparametric testing was used exclusively. Multiple comparisons were carried out using the Mann-Whitney U test. The α value for all tests was 0.05 and X^2 statistics, degrees of freedom and associated p-values were reported for all Kruskal-Wallis tests (Appendix A). Only p-values were reported for multiple comparisons.

4. RESULTS AND DISCUSSION

4.1 PIPELINE

4.1.1 Environmental Factors

The results of contingency table Chi Square analysis and log linear analysis of *Bromus inermis* cover class in conjunction with grazing intensity, vegetation cover type, slope and aspect showed no independence among factors, showing that although each factor contributed to the variation in *Bromus inermis* cover on the RoW none were partially independent or conditionally independent. When analyzed without considering *Bromus inermis* cover class a factor, environmental factors were not independent, supporting the suggestion that environmental factors were multi-colinear. Levels of one factor, vegetation cover for instance, changed with levels of another factor, such as grazing or aspect. This multi-colinearity makes interpretation of the impacts of main effects and the interactions between them impossible in this data set. Although the first objective could not be addressed in its entirety, the data set still shows that *Bromus inermis* has persisted 25 years after introduction, and that it will invade.

4.1.2 *Bromus inermis* Persistence and Invasion 25 Years After Introduction

Bromus inermis persists after introduction across all levels of grazing intensity, all aspects, varying slopes and all vegetation cover types. The presence of *Bromus inermis* 3 m from the pipeline RoW was not independent of cover class ($X^2 = 213.28$) with *Bromus inermis* being more likely found off the pipeline when cover class values on the pipeline are 3 through 6 (Figure 8), corresponding to percent cover values of 6 to 95%. The positive relationship between persistence and invasion is expected considering other studies showing increased invasion with increased propagule pressure (Rejmanek

and Richardson 1996, Lonsdale 1999). These results are important because they show the invasive potential of *Bromus inermis*, especially given that invasion occurs even at relatively low cover values (5 to 25%) in the propagule source area, in this case the RoW.

Data collected in the large-scale *Bromus inermis* study could not be used to determine which environmental factors increased a site's susceptibility to *Bromus inermis* invasion. Additional landscape scale factors including soil type, soil moisture, long-term climatic variation, historic grazing regime, and methods and timing of *Bromus inermis* introduction may be interacting to cause variation in *B. inermis* cover. Environmental factors evaluated in the study did not have strong enough effects to mask noise from other factors, and observations are on too coarse a scale to compare to the finer scale study. More control concerning sampling locations and number of sampling units, is necessary for this type of study to be of use in addressing the initial objective. Multi scale sampling (Stohlgren 1999) would also be useful to address plant community as well as landscape scale questions.

4.2 ANN AND SANDY CROSS CONSERVATION AREA

4.2.1 Plant Communities

The agglomerative cluster analysis followed by indicator species analysis grouped quadrats into three clusters, each with different indicator species (Table 4). *Bromus inermis* was the only indicator species for cluster three, and most quadrats with greater than 10% cover by *B. inermis*, were found in the same cluster (Figure 9). *Bromus inermis* and *Poa pratensis* are the only gramineae species present at greater than 2% cover in cluster 3 (Figure 10). Cluster one was typified by the dominant native species, *Festuca campestris*, while species that can be considered co-dominants such as *Danthonia parryi* (Moss and Campbell 1947, Looman 1982) were indicators in cluster 2. *Poa pratensis* is also an indicator species in the first cluster and, based on its abundance in relation to that of *F. campestris* and the other species present (Figure 10), it could also be considered a dominant species in cluster 1. All further characterization of the pattern of *Bromus inermis* invasion is based on differences between clusters one, two and three.

The grouping of clusters suggests the existence of two communities in the absence of *Bromus inermis*; one is characterized by dominants and the other by co-dominants commonly found in undisturbed rough fescue grassland. This second group of co-dominant species occurs on drier ecosites or is a remnant of an overgrazed plant community. Western wheatgrass (*Agropyron smithii*) is an indicator species in this community (Table 4) and is an indicator of historical overgrazing (Brown 1997). Additionally, Vujnovic et al. (2000) show the responsibility of small-scale disturbances such as grazing for decreases in dominance of *Festuca campestris*, leading to patchy increases in co-dominant species. Another hypothesis is that the second cluster is characterized by plants that are more competitive between fescue tussocks, which generally grow 15 to 30 cm across and 0.3 to 1 m high and associated plants grow in the inter-tussock space (Moss and Campbell 1947). Moss and Campbell (1947) have shown *Danthonia parryi* is an important species of local dominance in drier ecosites, including slopes and plant communities under moderate to heavy grazing intensity where *Festuca campestris* is at a competitive disadvantage (Looman 1982). Given the topographical characteristics of the study site and its long term grazing history, it is reasonable to expect a plant association typified by a low density of fescue tussocks with a *Danthonia-Agropyron-Koeleria* (Figure 10) community interspersed between them.

4.2.2 Changes in Diversity

Plant species composition and cover data collected at the mesoscale at the ASCCA study site revealed lower diversity, species richness and evenness in cluster 3 compared to that in clusters 1 and 2 (Figures 11 and 12). Species diversity and richness were highest in cluster 2, indicating effects of the absence of dominant species (Connell and Slatyer 1977). Statistically, evenness is significantly lower in cluster 3 than clusters 1 and 2 but the effect size is not very large. Therefore, lower diversity for cluster 3 seems to be a result of lower species richness rather than evenness, although evenness in cluster 3 is significantly different from that in clusters 1 and 2 (Figure 12).

Decreases in measures of diversity are consistent with other studies of plant invasions (Kolar and Lodge 2001) and more specifically, with invasions by *Bromus inermis* (Romo et al. 1990, Looman 1969). The large decrease in species richness in cluster 3 can be attributed to competitive exclusion of native species by *Bromus inermis*. Wilsey and Polley (2004) have shown decreases in evenness associated with increases in local

extinctions of rare species, and although this study was not designed to test that hypothesis, it could provide a hypothesis for the effects of *Bromus inermis* dominance. As *B. inermis* becomes more dominant, and evenness, a potential measure of that dominance, decreases, rare species begin to disappear and species richness decreases. The overall quantitative effect is a decrease in species diversity (Figure 12).

The effects of losses in biodiversity are widely disputed (Huston 1997, Symstad et al. 1998, Wardle et al. 1999). Some species-specific work has been carried out on the impacts of invaders, including resulting losses of biodiversity. Parker et al. (1999) highlight the importance of determining ecological impacts of invaders to prioritize eradication and control measures. *Agropyron cristatum* (crested wheatgrass), an invasive species in the Mixed Prairie Ecoregion has been associated with decreases in available nitrogen, total nitrogen and total carbon (Christian and Wilson 1999). Dormaar and Willms (2000) found that changes in soil chemical characteristics following cultivation and introduction of annual and perennial grasses were initially a result of cultivation but that long term changes would likely be associated with changes in species composition. Effects of *Bromus inermis* invasion on soil properties are as yet unknown, and it is possible that further study may reveal a relationship between *Bromus inermis* invasion and changes in the pattern of nutrient cycling in rough fescue grassland.

4.2.3 Shift in Dominance

Grime (1998) defines a dominant species as one that is proportionally high in abundance and accounts for a large proportion of the biomass in the community. Data from the characterization of *Bromus inermis* invasion pattern showed three distinct groupings of species, two characterized by dominants (Table 4, Figure 13). Cluster 1 has two dominant species, *Festuca campestris* and *Poa pratensis*. Cluster 3 is dominated by *Bromus inermis* co-existing with *Poa pratensis*, native forbs, and shrubs clearly representing a shift in dominance from native climax species to *Bromus inermis*.

The dominance diversity curve for cluster three shows the high proportional abundance of *Bromus inermis* in relation to all other species and the lower contribution all other species make to the total canopy cover, indicating dominance by *Bromus inermis* (Figure 13). The initial steep slope shows the large difference between abundance of *Bromus inermis* and abundance of the next most abundant species. Conversely, the curves

representing clusters 1 and 2 with very low *Bromus inermis* cover have flatter slopes, indicating higher diversity and less dominance in the community (Whittaker 1965) when compared at the same scale as *Bromus inermis*, an observation supported when the curves from clusters 1 and 2 are examined. The slope of the curve for cluster 1, a group characterized by two dominant species and lower diversity, is slightly steeper than that of the curve for cluster 2.

4.2.4 Theory of Dominance

Hutchinson (1957) defined the niche as an n-dimensional hypervolume where gradients of resources, space and time represent axes that define the space where species compete and evolve. Two species that occupy the same niche cannot coexist (Hutchinson 1957). It follows that *Bromus inermis* occupies the same niche as many of the dominant and subordinate members of the plant community present prior to invasion. Whittaker (1965) hypothesized that plants have evolved so that species in close proximity have slightly different environmental requirements and can, therefore, occupy different niche spaces, rather than having to exclude competitors from the only space available to them. As *Bromus inermis* becomes increasingly dominant, it appropriates a wider niche space in the community, effectively excluding many other community members (Whittaker 1965). This exclusion is supported by the dominance-diversity curve constructed for the community (Figure 13) and by changes in individual species abundance (Figure 10).

Studies conducted on *Festuca campestris* and *Bromus inermis* have shown that both species share similar niches, yet *Bromus inermis* may be a comparatively generalist species that is better able to compete under the anthropogenically-influenced disturbance regime in the Aspen Parkland. Grilz et al. (1994) found that *Bromus inermis* had higher germination than rough fescue over a wider yet similar range of moisture, temperature and light conditions. Nernberg and Dale (1997) found that *Bromus inermis* was less affected by water stress than five other native species more adapted to drought than *Festuca campestris*. Brown (1997) found that heavy defoliation did not stress *Bromus inermis* as evidenced by tiller density, etiolated regrowth and total nonstructural carbohydrates. In contrast, rough fescue grassland is especially sensitive to overgrazing (Dormaar and Willms 1990). The results of these studies show that *Bromus inermis* is

able to thrive across natural gradients of resources and disturbance where the native plant community is more severely affected, and thus maintain competitive advantage.

4.2.5 Poa pratensis

The dominance of *Bromus inermis* can be contrasted with the role played by *Poa pratensis* in the same plant community. The proportional abundance of *Poa pratensis* remains relatively unchanged in communities characterized by dominant species (Figure 10). It is only greatly reduced in cluster 2 where dominance is lower. In plant associations with the lowest *Bromus inermis* cover, clusters 1 and 2, other species are present whose abundance greatly decreases inversely proportional to that of *Bromus inermis* (Figure 10). These species do not exhibit the same relationship with the abundance of *Poa pratensis*. Further study is required to determine in which communities and under what conditions *P. pratensis* competitively excludes other species, even though it appears not to in this community.

Willoughby and Alexander (2000) and Bailey (1975) found that overgrazing allowed *Poa pratensis* to invade rough fescue prairie. In their study, a return to rough fescue dominated grassland was considered unlikely. Brown (1997) found that *Poa pratensis* increased under heavy grazing and herbicide treatments, and concluded that overgrazing could cause invasion in rough fescue grassland. *Poa pratensis* is considered naturalized in Alberta (McClay 2004) although whether it has actually successfully invaded depends on the definition of naturalized in use. According to Mack et al. (2000), the definition of a naturalized species is an introduced species that maintains populations without human aid and naturalization is a precursor to invasion. Conversely, Richardson et al. (2000) define naturalized plants as plants that maintain self-sustaining populations but do not invade surrounding ecosystems. Considering the demonstrated potential of *Poa pratensis* to spread (Donkor et al. 2002), it can be considered invasive, according to the first of the above definitions. Rejmanek and Richardson (1996) state that latitudinal range is the best predictor for herbaceous-species-invasion potential. Given that *Poa pratensis* is widely distributed throughout Alberta, it could be a potential invader, especially if it is released from competition with dominant species. This conclusion is not supported by the data collected at the Ann and Sandy Cross Conservation Area. *Poa pratensis* significantly decreased in abundance in

the absence of dominant species (Figure 10). Further study is required to determine the invasive potential of *Poa pratensis* in rough fescue grassland plant communities.

4.2.6 A Potential Mechanism of Dominance

While experimental determination of competition intensity was not an objective of this study, it is possible to infer a potential mechanism of dominance from the structural characteristics of the plant community. In the future, this hypothesis could be tested in a controlled environment to increase understanding of the competitive mechanism of *Bromus inermis*.

Overall, canopy cover was greater in the presence of *Bromus inermis* although stem cover was reduced (Figures 14 and 15). At the invasion edge, the maximum canopy height was greater for *Bromus inermis* (Figure 16) although it was less dense (Figure 17). Given that *Bromus inermis* is dominant in the canopy, the hypothesis that *it* is a better competitor for light is reasonable. In addition, the proportion of *Festuca campestris* in the canopy increases as that of *Bromus inermis* decreases (Figure 18). This phenomenon is best illustrated in the transition zone because the absence of brome in a fescue patch and vice versa is tautological given the sampling design. The number of stems along transects from *Bromus inermis* patches to fescue patches increased (Figure 19). These results are not surprising, however the presence of *Bromus inermis* leaves in the canopy in native patches should be noted (Figure 18). This observation supports the hypothesis that above ground competition is potentially important during *Bromus inermis* invasion of rough fescue prairie. Awada et al. (2003) found that *Bromus inermis* is relatively shade-tolerant and while the shade tolerance of *Festuca campestris* is unknown, given its position as the dominant species in the community, outcompeting shorter stature native plants for light, it can be hypothesized that it is not shade tolerant. In addition, *Festuca campestris* is not found in the forest understory of the Aspen Parkland whereas *Bromus inermis* is (Moss and Campbell 1947). The effects of below ground competition in this system are unknown, although Vujnovic et al. (2000) hypothesized that they are important, given the growth limiting soil nitrogen levels in fescue dominated grassland. Further study should focus on quantification and comparison of above and below ground competition between *Bromus inermis* and rough fescue.

Although light competition is a potential explanation for competitive exclusion of native species by *Bromus inermis*, litter depth was significantly greater under *Bromus inermis* cover than under native vegetation or in the transition between the two cover types (Figure 20). This indicates that perhaps *Bromus inermis* is able to prevent the establishment of other species by decreasing the amount of bare ground and light required for colonization while modifying the soil environment to create better conditions for rhizomatous growth. Litter lowers soil temperature and increases soil moisture through increased water holding capacity and reduced evaporation from the soil surface (Naeth et al. 1991). Additionally, *Bromus inermis* seed is adapted to germinate under cool moist conditions found under deep litter (Grilz et al.1994).

4.3 LANDSCAPE, MESO AND MICRO SCALE INVASION OF *BROMUS INERMIS*

At the landscape scale *Bromus inermis* persisted in native pastures 25 years after introduction on to a pipeline RoW, and *Bromus inermis* invaded native pastures where it maintained between 5 and 25% cover off the pipeline. The considerable likelihood of invasion demonstrated by these results is consistent with the aggressive characteristics of *Bromus inermis*, which is a prolific seed producer (Toynbee 1987), grows more quickly, and produces more biomass than native species (Smoliak and Johnston 1968). It is also widely adaptable (Nernberg and Dale 1997, Grilz et al. 1994) and spreads by rhizomes once established, decreasing the growth and abundance of native flora (Romo et al. 1990).

In the ASCCA meso scale study, results of *Bromus inermis* invasion include decreased plant community diversity, loss of *Festuca campestris*, the native dominant species, and increased dominance in the *Bromus inermis* occupied plant community. These results are consistent with those of other researchers studying *Bromus inermis* invasion (Romo et al. 1990). Study at the invasion edge or mesoscale showed that *Bromus inermis* is a taller species and is present in the canopy in native patches, pointing toward above ground competition as a potential mechanism of dominance. Below ground competition has been cited as potentially important in this community by other researchers (Vujnovic et al. 2000). Given the rhizomatous nature of *Bromus inermis*, rhizomes may also extend into the native plant community competing for nutrients and moisture (Looman 1969, Romo et al. 1990).

The results of the pipeline study show that *Bromus inermis* persists and does invade where it is introduced, regardless of variation in aspect, slope, vegetation cover type and grazing regime. It likely invades through above and potentially, below ground competition, and the effects of invasion are reductions in diversity in native plant communities and loss of the dominant native species. Disturbance plays an important role in invasion, either as the vector of introduction, as in the case of the pipeline, or as the factor putting the dominant native species at a competitive disadvantage, as in the case of grazing (Hobbs and Huenneke 1992, Willms and Quinton 1995, Burke and Grime 1996, Bogen et al. 2003). Linear disturbances, such as pipelines and roadways, are particularly important vectors of introduction given the long invasion edge created (Rentch et al. 2005).

5. MANAGEMENT CONSIDERATIONS

Considerable work has been done on the eradication and control of *Bromus inermis* in fescue grasslands. For example, spring burning reduced cover of *Bromus inermis,* although success is dependent on the presence of warm season native grasses and adequate soil moisture (Willson and Stubbendieck 2000; Blankespoor and Larson 1994). Willson and Stubbendieck (2000) found competition from warm season native species an important factor in reducing *Bromus inermis* dominance after burning. Conversely, Grilz and Romo (1994) found that neither spring nor autumn burning reduced *Bromus inermis* dominance in fescue prairie. Their hypothesis supports the work of previous studies because fescue grassland is dominanted by C_3 species, unlike tallgrass prairies in Nebraska and Oklahoma (Grilz and Romo 1994). Native C_3 dominants are also suppressed by fire and gain no competitive advantage through early season burns. Brown (1997) found that defoliation treatments stimulated an increase in *Bromus inermis* tiller density, glyphosate application reduced but did not eliminate *Bromus inermis,* and burning did not enhance glyphosate effectiveness. Although herbicide application was an effective method of control, careful attention had to be paid to the effects on desirable species (Brown 1997). In light of the importance of competition from native species in *Bromus inermis* control and elimination (Willson and Stubbendieck 2000; Blankespoor and Larson 1994; Grilz and Romo 1994), eradication strategies should be directed

toward enhancement of native plant communities as well as elimination of *Bromus inermis*.

To enhance the competitive ability of native plant communities as part of eradication strategies, the niches occupied by *Bromus inermis* and *Festuca* spp. and their competitive strategies must be better understood. Observation of physiological and ecological characteristics of *Bromus inermis* and *Festuca* spp. dominated plant communities as well as controlled experimentation with eradication techniques led Brown (1997) to postulate the following mechanisms of invasion. Rapid early spring growth allows *Bromus inermis* to take up nutrients and moisture in the absence of competition from native species that remain dormant until later in the spring. Aggressive rhizome production results in an increase in the spatial extent of below ground competition and seed dispersal and establishment on small soil disturbances provide foci for further invasion. High litter production possibly depletes the seed bank and restricts germination of species dependent on seed dispersal for establishment of new individuals. *Bromus inermis* also has high biomass yield and is taller than most native species, permitting it to out-compete shorter grasses for light. The results of this study support the hypothesis that light competition is important, however, further work is necessary to determine the mechanism of competition in rough fescue grassland.

Bromus inermis has proven to be an excellent forage crop and it persists without frequent reseeding (Casler and Carlson 1995). However this and other studies have shown that *Bromus inermis* persists and invades in rough fescue grassland (Romo et al. 1990, Brown 1997). *Bromus inermis* is likely able to dominate because it is able to occupy more niche space than *Festuca campestris* and is less affected by common disturbances in the Aspen Parkland such as fire and grazing. Given these results *Bromus inermis* should not be introduced where conservation of native rough fescue grassland is a priority.

6. CONCLUSIONS

- *Bromus inermis* persists and invades in the Aspen Parkland Ecoregion in the long term (25 years), irrespective of grazing regime, slope, aspect and vegetation cover type.

- The effects of *Bromus inermis* invasion include reductions in species diversity and its components, species richness and evenness.
- *Bromus inermis* should not be introduced where conservation of rough fescue grassland is a priority because invasion potential is high as is the likelihood of adverse consequences for the native plant community.

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III. SYNTHESIS

1. RESEARCH RESULTS

The study of *Bromus inermis* invasion at landscape, macro and meso scales in the Aspen Parkland Ecoregion of Alberta showed that: *Bromus inermis* is persistent across a wide range of environmental variation, that invasion occurs when a propagule source is present, that impacts of invasion include decreases in plant species diversity, and that when brome invades it becomes a dominant rather than subordinate or coexisting species. In the context of the pipeline and Ann and Sandy Cross Conservation Area (ASCCA) studies, disturbance was important as a vector of introduction. At the ASCCA, historical grazing disturbance was potentially important in reducing the competition and abundance of the native dominant species, *Festuca campestris.*

This study described the invasive potential of *Bromus inermis* at a landscape scale and the pattern of invasion at macro and meso scales. Illustrating the extent and pattern of brome invasion in Alberta was important to better direct further research concerning community invasibility, the invasive potential of *Bromus inermis* and the impacts and associated mechanisms of invasion. This research has shown that all plant communities in the Aspen Parkland are potentially invasible, that *Bromus inermis* has high invasion potential and that complete transformation of rough fescue grassland is a likely outcome of invasion.

2. FUTURE RESEARCH

2.1 *BROMUS INERMIS*

Much research has been carried out on *Bromus inermis* as a forage (Casler and Carlson 1995), its management as a forage (Donkor et al. 2002) and its eradication in rough fescue and tallgrass prairie (Blankespoor and Larson 1994, Grilz and Romo 1994, Willson and Stubbendieck 2000), but very little has been done on its community level impacts on native soils and vegetation. Further research should attempt to elucidate the competitive mechanisms of *Bromus inermis* including response to resource pulse, resource limitation and small scale disturbance, as well as efficiency of above and below ground competition. Knowing how *Bromus inermis* might modify its environment, either

to better suit its requirements or to the disadvantage of its competitors, is important. The response of *Bromus inermis* to defoliation is well understood (Donkor et al. 2002) but more research is required to determine how it takes advantage of bare patches in the community, either from decreased cover or soil disturbance (Blankespoor and May 1996). This particular response could be of great importance given the patchy nature of rough fescue grassland communities. *Bromus inermis* could take advantage of the absence of fescue in the inter-tussock space and preferentially invade there, slowly choking out the large fescue plants.

2.2 *FESTUCA CAMPESTRIS* AND *FESTUCA HALLII*

Much is also understood about the general ecology of *Festuca campestris* and *Festuca hallii* (Moss and Campbell 1947, Looman 1967) grassland but very little work has been done on these grasses in direct competition with *Bromus inermis*. The response of *Festuca* spp. to grazing is well known (Willms and Quinton 1995) but the direct relationship between *Bromus inermis* invasion success and grazing intensity has not been studied. *Festuca* spp. are rooted tufted perennials and are considered climax species. Thus, their response to direct competition should also be studied given that they have evolved in a system where they are the only large stature dominant species. Additionally, the competitive mechanisms of *Festuca* spp. should be studied in comparison with those of *B. inermis* listed above. The dispersal and establishment characteristics of *Bromus inermis* and *Festuca* spp. have been well studied although not together. The study of quantitative differences in dispersal and establishment limitation for both species would be an appropriate subject on which to carry out meta-analysis.

2.3 THE LANDSCAPE SCALE

Studying invasion at the landscape scale is important to focus conservation and eradication efforts where they are most needed and most likely to succeed (With 2002). Given the large number of points on the landscape where *Bromus inermis* has been introduced as a forage or reclamation species, landscape scale research is especially important. Variation in dispersal rate, invasion rate, and degree of persistence over the landscape scale range of topography, plant community type, soil type and disturbance regime should be both modeled and studied empirically. This type of study will pinpoint

areas at high risk of invasion to which conservation efforts should be directed. It will also highlight combinations of environmental factors that will either promote or inhibit continuing invasion. Eradication would logically be more successful where invasion is inhibited compared to areas where invasion is likely to continue in the long term.

2.4 EMPIRICAL RESEARCH

The above research should be carried out empirically using controlled experiments or at least controlled observation. Without empirical results, it is difficult to assess and test for mechanisms. Elucidating mechanisms is important in an applied and theoretical sense because quantitatively showing the mechanism behind observed impacts can support or disprove general ecological theories and can best direct land managers when dealing with the species of interest. Examples of appropriate research direction include transplanting experiments, removal experiments and controlled greenhouse studies to observe smaller scale effects. At the landscape scale, control in field studies becomes more difficult but attention to independence of sample units and appropriate number of sample units is critical. Additional methods such as GIS, remote sensing and air photo interpretation are of use in this large scale type of study. Observational studies have merit in directing future research but it is from well-designed empirical research on specific pattern and process that the most reliable conclusions about process behind easily observable patterns can be made.

3. CONCLUSIONS

The study of brome invasion at multiple scales in the Aspen Parkland Ecoregion of Alberta demonstrated that *Bromus inermis* is an aggressive invader where it is introduced, is likely to persist, and has definite impacts on native plant community structure. To inform conservation and eradication measures, further empirical research is needed, especially on mechanisms of competition and niche opportunity for *Bromus inermis* and *Festuca* spp. at meso, macro and landscape scales. Fridley et al. (2004) discussed the importance of testing results against appropriate null models, and though he was speaking specifically about the relationship between invasibility and diversity, this lesson is applicable to the study of invasions in general. This and other observational studies help to develop those null models so they can be tested against in

future studies. In that context, an important result of this study is the generalization that brome persists when it is introduced. This generalization can be used as a null model in future landscape scale studies of this species.

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With, K.A. 2002. The landscape ecology of invasive spread. Conservation Biology 16:1192-1203.

Table 1. *Bromus inermis* cover classes used for pipelines 1 and 2.

Cover Class	Percent Cover	Midpoint
1	0	0
2	1 to 5	3
3	6 to 25	15
4	26 to 50	37.5
5	51 to 75	62.5
6	76 to 95	85
7	96 to 100	97.5

Table 2. Dominant plant community types along study pipelines 1 and 2 in the Aspen Parkland.

Cover Type	Description
Rough Fescue	Grassland dominated by *Festuca halii* and *Danthonia parryi*
Dry Mixed Grass	Grassland dominated by *Stipa Agropyron* species
Rough Fescue - Dry Mixed Grass	Transition between dry mixed grass and rough fescue grasslands
Poa pratensis	Grassland dominated by *Poa pratensis*
Poa pratensis - Dry Mixed Grass	Grassland dominated by *Stipa* and *Agropyron* species and *Poa pratensis*
Poa pratensis - Rough Fescue	Grassland dominated by *Festuca halii* and *Poa pratensis*
Woody Shrub	Shrubland dominated by *Symphoricarpos occidentalis*, *Rosa acicularis* or *Elaeagnus commutata*
Woody Shrub - Rough Fescue	Shrubland with rough fescue
Woody Shrub – *Poa pratensis*	Shrubland with *Poa pratensis*
Upland Aspen Forest	Aspen dominated forest on north facing slopes
Lowland Aspen Forest	Aspen dominated forest on topographical lows
Wetland and Riparian	Wetland and riparian vegetation dominated by sedges, rushes and willows

Table 3. Grazing impact assessment matrix for the pipelines 1 and 2.

	Low	Medium	High
Seedheads	> 50%	30 to 50%	< 30%
Litter Cover	> 65%	65 to 35%	< 30%
Decreasers	> 60%	40 to 60%	< 40%
Overall Intensity	Average of 3 measures of intensity		

Table 4. Indicator species for the macroscale study at the ASCCA with associated indicator and p-values.

Species	Cluster	IV	p
Artemisia ludoviciana	1	25.2	0.002
Aster spp.	1	23.5	0.001
Festuca campestris	1	42.3	0.001
Galium boreale	1	34.4	0.001
Poa pratensis	1	52.1	0.001
Agropyron smithii	2	31.9	0.001
Anemone patens	2	13.6	0.002
Aster ericoides	2	27.1	0.001
Cirsium arvense	2	50.6	0.001
Danthonia parryii	2	49.3	0.001
Koeleria macrantha	2	16.5	0.001
Lupinus sericeus	2	53.9	0.001
Monarda fistulosa	2	14.1	0.004
Rosa acicularis	2	26.8	0.001
Bromus inermis	3	97.2	0.001

Figure 1. Ecoregions of western Canada and the three study sites, depicted with red stars, used to evaluate *Bromus inermis* persistence and invasion in Alberta Aspen Parkland. Adapted from Fast (2005).

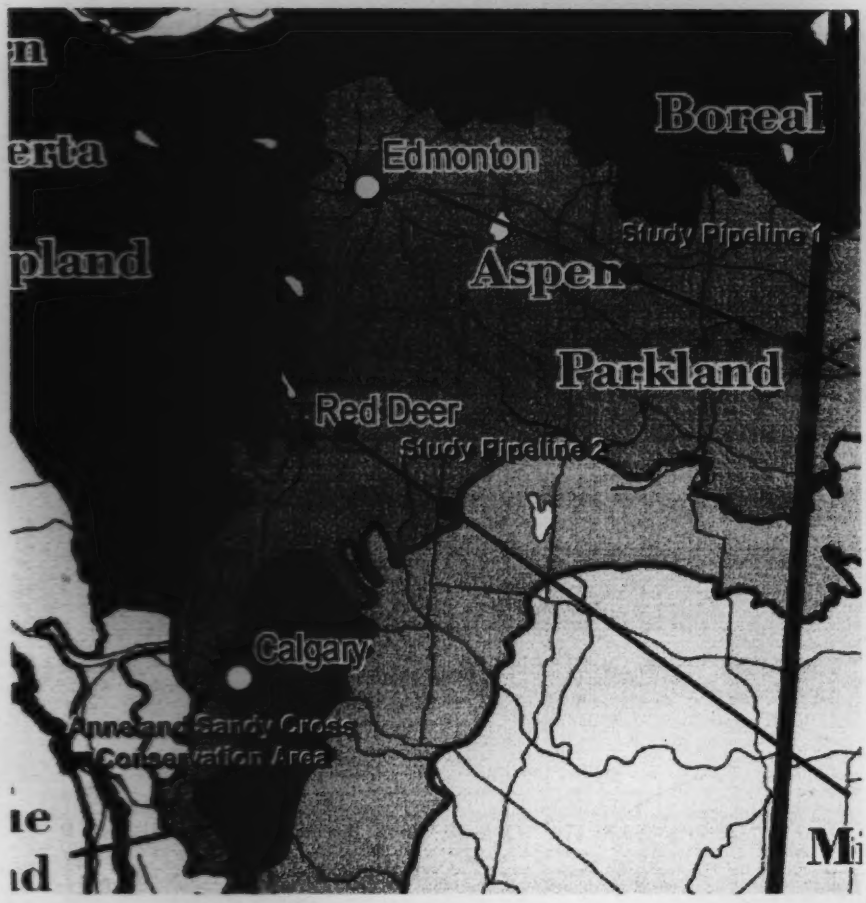

Figure 2. Study site locations for the evaluation of *Bromus inermis* persistence and invasion within Alberta Aspen Parkland. The ASCCA study site is depicted with a red star. Pipelines are depicted with red lines and portions evaluated are demarcated by red dots. Adapted from Fast (2005).

Figure 3. *Bromus inermis* invasion on a 25 year old pipeline RoW (study pipeline 2). Darcy Henderson photo credit.

Figure 4. ASCCA study site from the toe of the slope looking northwest. Ken Parker photo credit.

Figure 5. ASCCA study site from the toe of the slope looking north. Ken Parker photo credit.

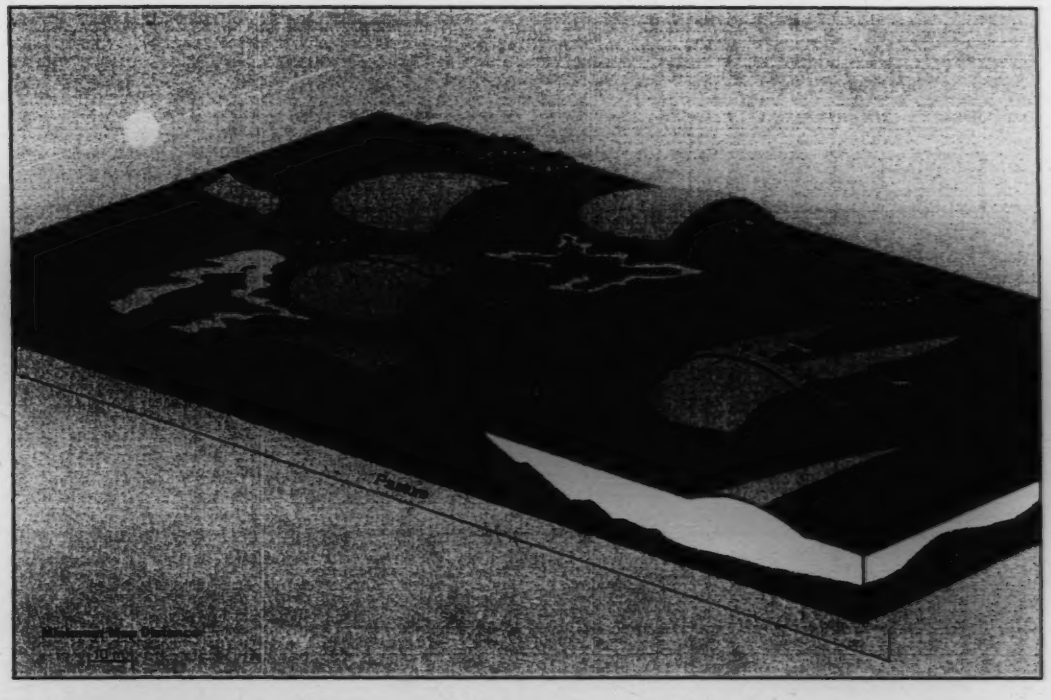

Figure 6. Sampling units for the pipeline study. Adapted from Henderson et al. (2003).

Figure 7. Invasion edge at ASCCA, looking from native patch to brome patch. Ken Parker photo credit.

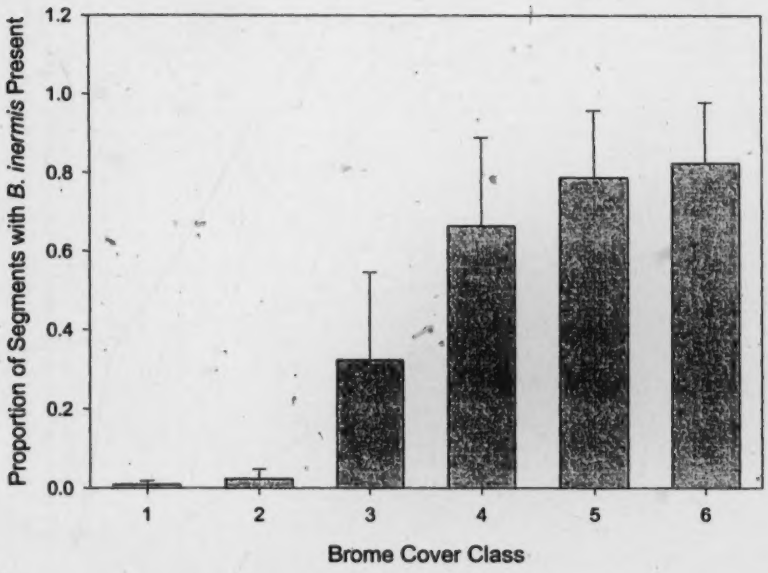

Figure 8. *Bromus inermis* cover class on the pipeline versus the proportion of segments with *Bromus inermis* present off the pipeline.

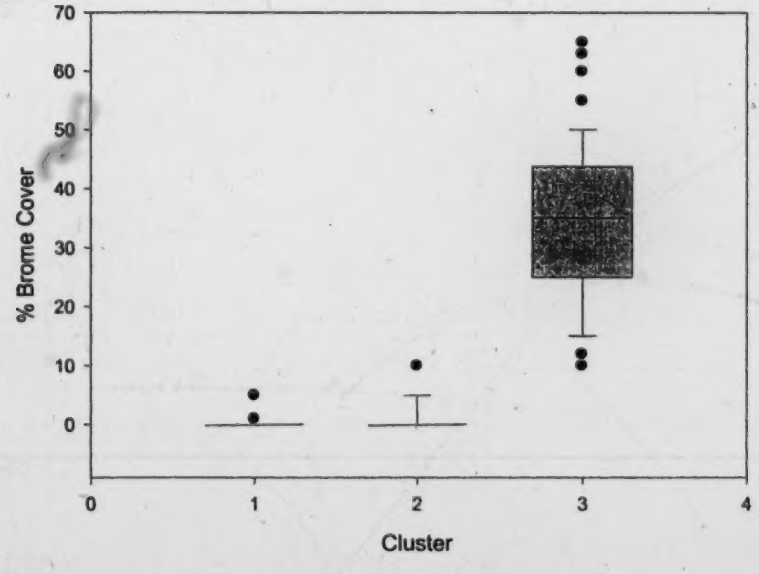

Figure 9. Box plots showing the range of *Bromus inermis* data for clusters 1 to 3.

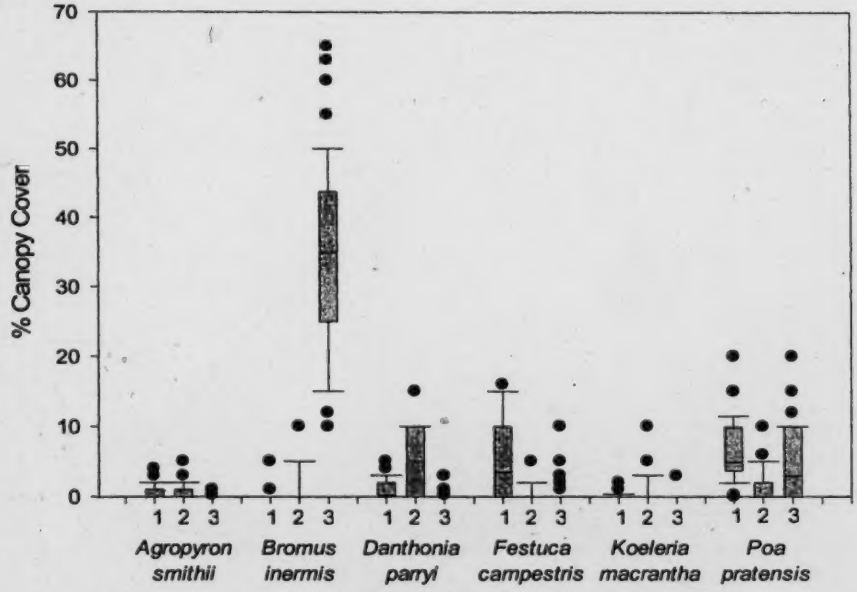

Figure 10. Range of canopy cover by species data in clusters 1, 2 and 3 at the ASCCA.

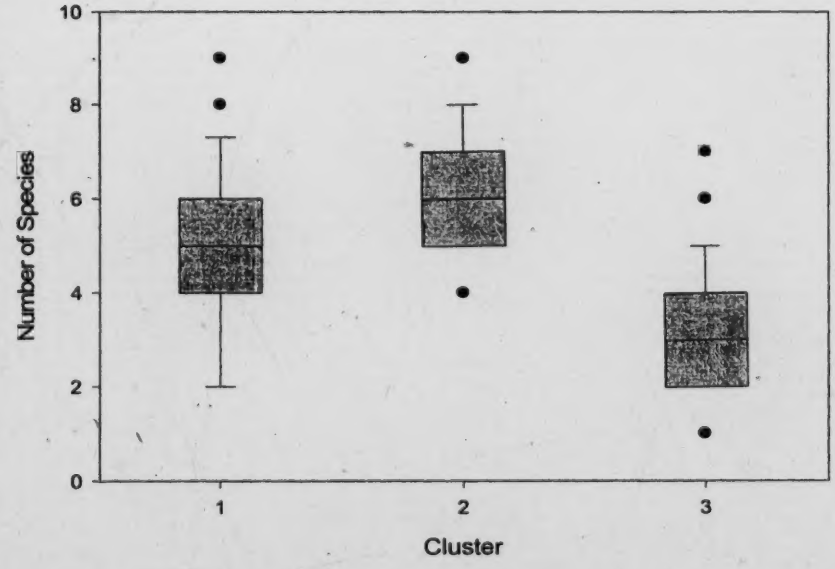

Figure 11. Range of species richness data in clusters 1, 2 and 3 at the ASCCA.

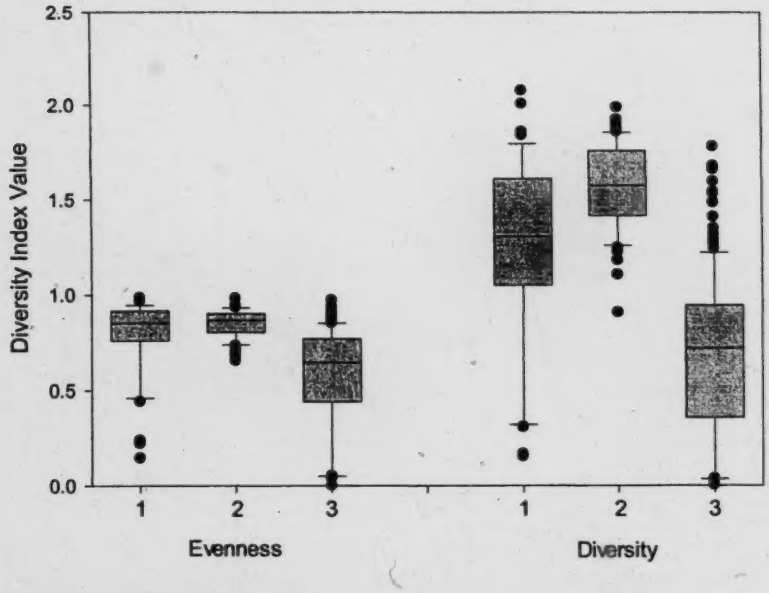

Figure 12. Range of species evenness and diversity in clusters 1, 2 and 3 at the ASCCA.

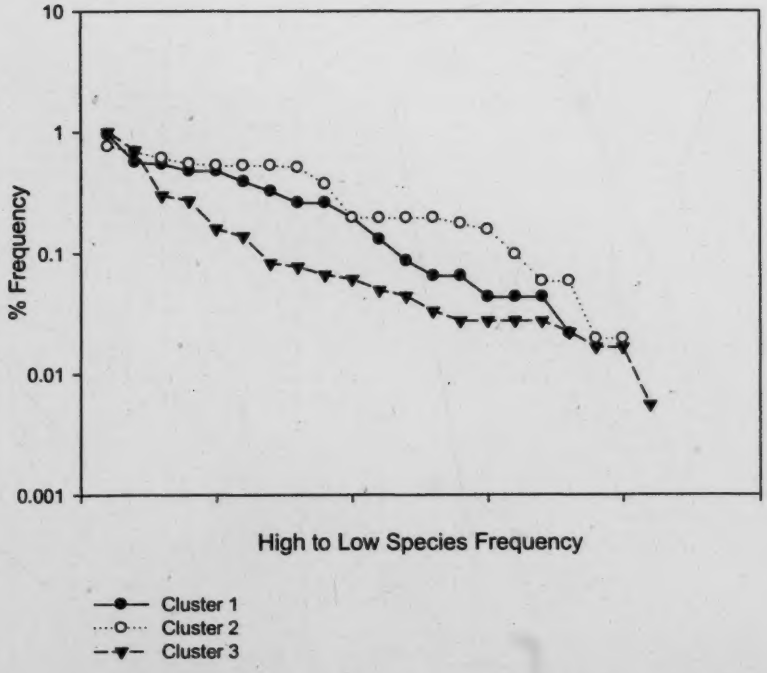

Figure 13. Dominance diversity curve for clusters 1, 2 and 3 at the ASCCA.

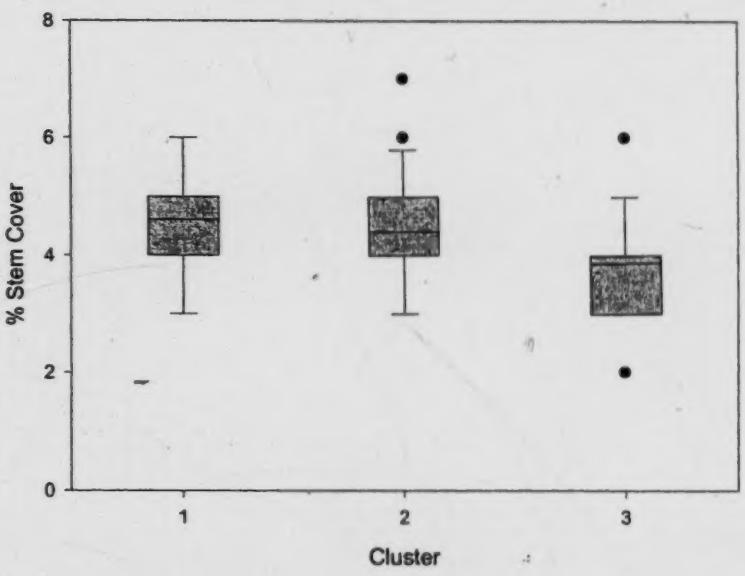

Figure 14. Range of stem cover data in clusters 1, 2 and 3 at the ASCCA.

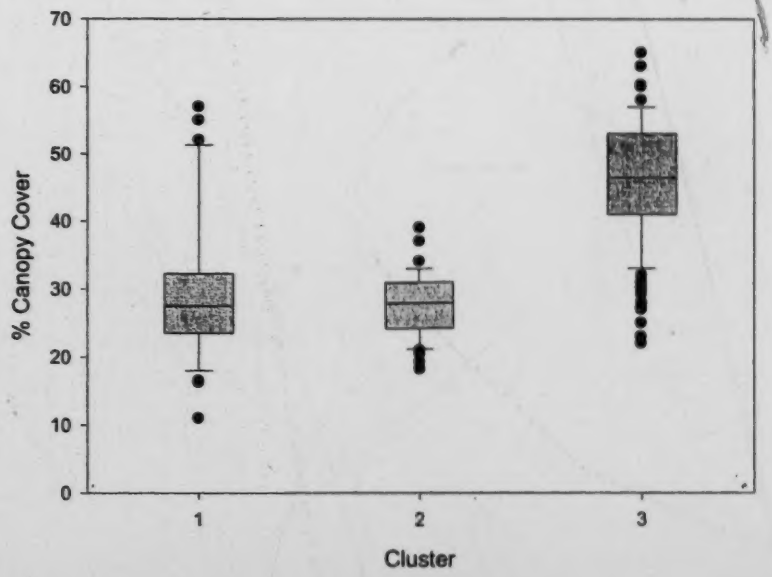

Figure 15. Range of canopy cover data in clusters 1, 2 and 3 at the ASCCA.

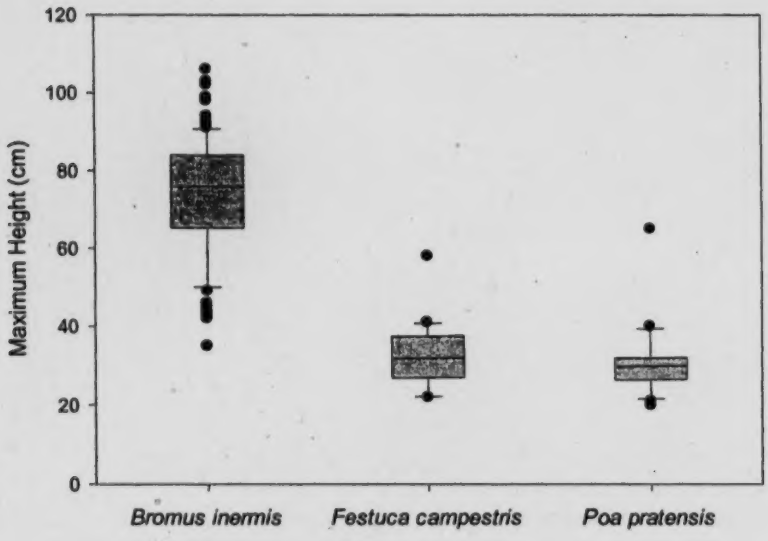

Figure 16. Range of maximum canopy height data for three species at the ASCCA.

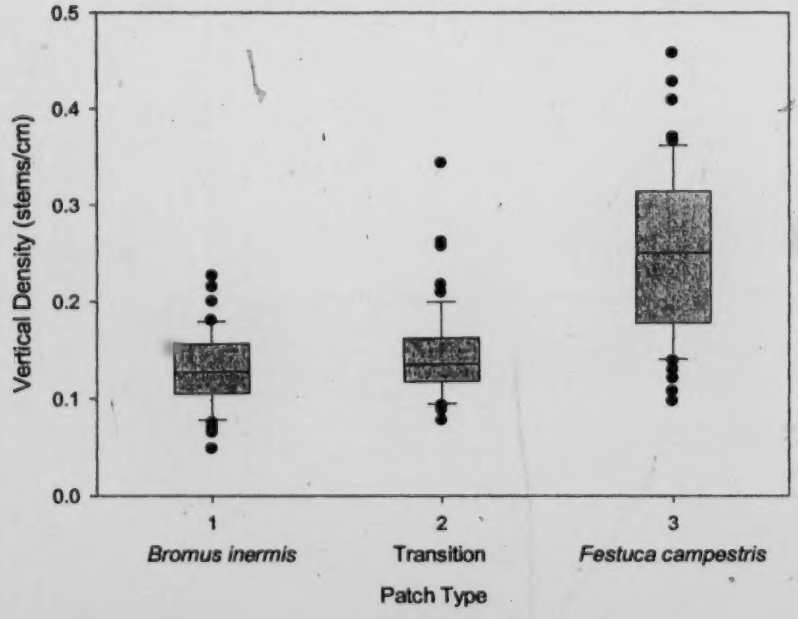

Figure 17. Range of vertical density (cm) in *Bromus inermis*, transition and *Festuca campestris* patches at the ASCCA.

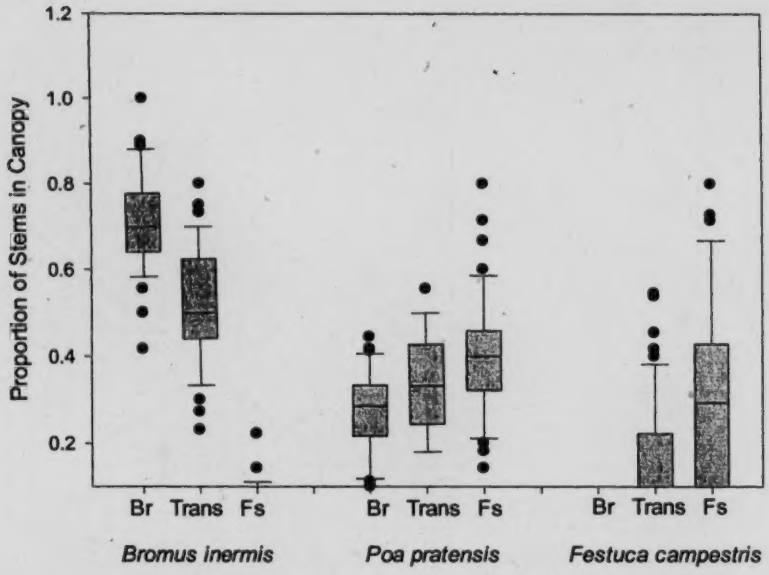

Figure 18. Proportion of total canopy stems by species from *Bromus inermis* to *Festuca campestris* patches. Br denotes *B. inermis*, Trans denotes Transition and Fs denotes *Festuca campestris*.

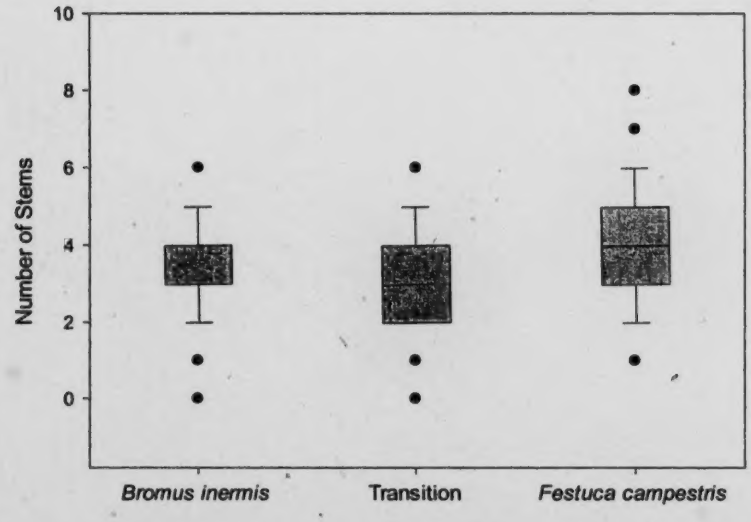

Figure 19. Range of stem count on ground transects in *Bromus inermis*, transition and *Festuca campestris* patches at the ASCCA.

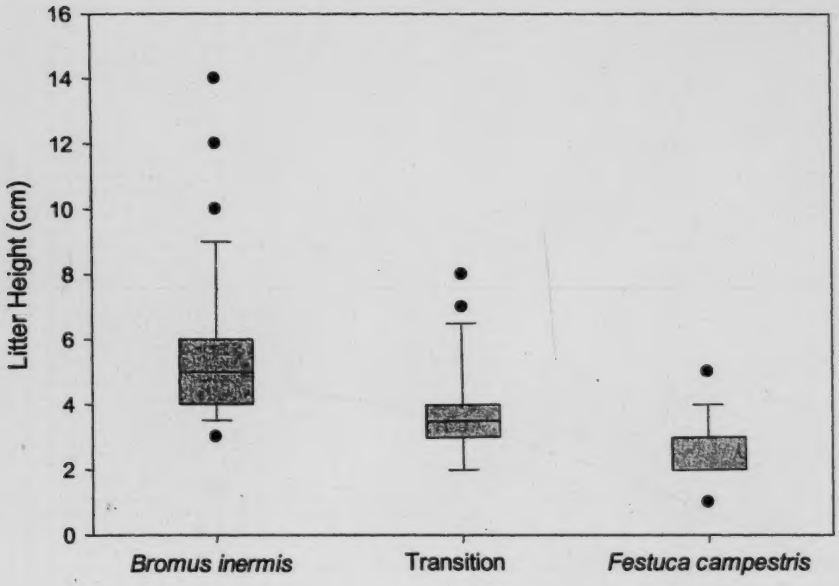

Figure 20. Litter height in *Bromus inermis,* transition and *Festuca campestris* patches at the ASCCA.

APPENDIX A

Table A1. Vegetation and soils description for pipelines 1 and 2

Pasture Location	Vegetation	Soil Series	Great Group
NW 22-43-05-04	Aspen/Snowberry-Saskatoon, June/Wheatgrass	N/A	Orthic Dark Brown Chernozem
SE 22-43-05-04	Aspen/Snowberry-Saskatoon, Needlegrass	N/A	Orthic Dark Brown Chernozem
SW 23-43-05-04	Poplar/Dogwood-Willow,	N/A	Orthic Dark Brown Chernozem
SE 23-43-05-04	Aspen/Snowberry-Saskatoon	N/A	Orthic Dark Brown Chernozem
SE 18-42-03-04	Rough Fescue, June-Wheatgrass	N/A	Orthic Dark Brown Chernozem
NE 05-41-02-04	Needlegrass, June-Wheatgrass, Aspen/Snowberry-Saskatoon	N/A	Orthic Dark Brown Chernozem
NW 04-41-02-04	Stream margins	N/A	Orthic Dark Brown Chernozem
SW 25-37-25-04	Dry Aspen, Mesic shrubland complex	Angus Ridge	Eluviated Black Chernozem
NE 24-37-25-04	Mesic Aspen-Poplar forest, Mesic grassland, Wet meadow	Angus Ridge	Eluviated Black Chernozem
NW 11-37-24-04	Mesic grassland, Mesic Aspen-Poplar forest, Wet meadow	Angus Ridge	Eluviated Black Chernozem
SW 11-37-24-04	Mesic grassland, Mesic shrubland, Dry Aspen	Angus Ridge	Eluviated Black Chernozem
NE 02-37-24-04	Mesic grassland, Dry Aspen	Angus Ridge	Eluviated Black Chernozem
SE 25-35-22-04	Dry Aspen-Mesic grassland complex	Elnora	Orthic Black Chernozem
SW 25-35-22-04	Dry Aspen-Mesic grassland complex	Elnora	Orthic Black Chernozem
NE 09-35-21-04	Mesic grassland-Mesic shrubland complex	Elnora	Orthic Black Chernozem
NW 25-34-21-04	Mesic grassland-Mesic shrubland complex, Wet meadow	Scollard	Orthic Dark Brown Chernozem
SW 29-34-20-04	Native pasture	Hughenden	Orthic Dark Brown Chernozem
NW 20-34-20-04	Native pasture	Hughenden	Orthic Dark Brown Chernozem
NW 21-34-20-04	Mesic grassland-Dry Aspen complex	Hughenden	Orthic Dark Brown Chernozem
SW 21-34-20-04	Mesic grassland-Dry Aspen complex	Hughenden	Orthic Dark Brown Chernozem
NE 15-34-20-04	Wet shrubland-mesic grassland	Hughenden	Orthic Dark Brown Chernozem
12-34-20-04	Wet shrubland/Dry Aspen/Mesic grassland complex (Rumsey Natural Area)	Halkirk	Dark Brown Solodized Solonetz
07-34-19-04	Wet shrubland/Dry Aspen/Mesic grassland complex (Rumsey Natural Area)	Hughenden	Orthic Dark Brown Chernozem
05-34-19-04	Wet shrubland/Dry Aspen/Mesic grassland complex (Rumsey Natural Area)	Hughenden	Orthic Dark Brown Chernozem
SW 02-32-16-04	Mesic grassland-Mesic shrubland complex	Hughenden	Orthic Dark Brown Chernozem
NW 35-31-16-04	Mesic grassland-Mesic shrubland complex	Dolcy	Orthic Dark Brown Chernozem
NE 35-31-16-04	Mesic grassland-Mesic shrubland complex	Dolcy	Orthic Dark Brown Chernozem

Adapted from Alliance Pipelines (1999) and BP Amoco (2000).

Table A2. Statistics for the ASCCA

Test	Kruskal-Wallis ANOVA by Ranks			Multiple Comparisons		
	Clusters 1, 2 and 3			1 vs 2	2 vs 3	1 vs 3
	X^2	df	p-value	p-value	p-value	p-value
% Canopy cover of *Agropyron smithii*	88.137	2	0.000	0.062	0.000	0.000
% Canopy cover of *Bromus inermis*	195.193	2	0.000	0.061	0.000	0.000
% Canopy cover of *Danthonia parryi*	116.877	2	0.000	0.001	0.000	0.000
% Canopy cover of *Festuca campestris*	105.292	2	0.000	0.047	0.000	0.000
% Canopy cover of *Poa pratensis*	47.693	2	0.000	0.000	0.000	0.001
% Canopy cover of *Koeleria macrantha*	29.732	2	0.000	0.86	0.000	0.001
Species richness	120.605	2	0.000	0.000	0.000	0.000
Evenness	87.932	2	0.000	0.694	0.000	0.000
Shannon-Weiner diversity index	126.026	2	0.000	0.000	0.000	0.000
% Stem cover	32.027	2	0.000	0.209	0.000	0.000
% Canopy cover	124.396	2	0.000	0.800	0.000	0.000
	By species: (BROINE, FESCAM and POAPRA)			BROINE vs FESCAM	FESCAM vs POAPRA	BROINE vs POAPRA
Maximum canopy height	93.498	2	0.000	0.000	0.439	0.000
	By patch type : (*Bromus inermis*, transition and fescue)			*Bromus inermis* vs Transition	Transition vs Fescue	Fescue vs *Bromus inermis*
Vertical density	63.053	2	0.000	0.139	0.000	0.000
% *Bromus inermis* stems in canopy	128.086	2	0.000	0.000	0.000	0.000
% *Poa pratensis* stems in canopy	23.726	2	0.000	0.018	0.014	0.000
% *Festuca campestris stems* in canopy	59.727	2	0.000	0.000	0.000	0.000
Number of stems at ground level	26.068	2	0.000	0.647	0.000	0.000
Litter height	74.759	2	0.000	0.000	0.000	0.000